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Life history divergence of sympatric diploid and polyploid populations of brine shrimp *Artemia parthenogenetica*

Lei Zhang, Charles E. King

Department of Zoology, Oregon State University, Corvallis, OR 97331-2914, USA

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Abstract. In order to study how polyploidy affects life history patterns in animals, we have examined sympatric diploid and polyploid brine shrimp (*Artemia parthenogenetica*) from China, Italy and Spain under laboratory conditions. At optimal temperature and salinity (25° C and 90 ppt), diploids from the three populations had much higher intrinsic rates of increase, higher fecundity, faster developmental rates, and larger brood sizes than their sympatric polyploids. The Chinese and Italian populations were selected for further analysis to determine the life history responses of diploids and polyploids to temperature and salinity changes. Under intermediate and high salinities, Chinese and Italian polyploids produced most of their offspring as dormant cysts while their sympatric diploids produced most of their offspring as nauplii. This relationship is reversed in the Spanish diploid-polyploid complex. For the Chinese population at 25° C, pentaploid clones had higher developmental rates than diploid clones at 35 ppt; at 90 ppt, diploid clones had higher developmental rates than the pentaploids. Italian diploids and tetraploids had different responses to variation in both temperature (25° C and 31° C) and salinity (30 ppt and 180 ppt). Our results demonstrate that relative fitness of the two cytotypes is a function of environmental conditions and that sympatric diploids and polyploids respond differently to environmental changes. Chinese and Italian polyploids are expected to have lower fitness than their sympatric diploids when the physical environment is not stressful and when intraspecific competition is important. However, polyploids may have advantages over sympatric diploids in stressful habitats or when they encounter short-term lethal temperatures. These results suggest that polyploid *Artemia* have evolved a suite of life-history characteristics adapting them to environments that contrast to those of their sympatric diploids.

Key words: *Artemia* – Polyploidy – Population dynamics – Life history evolution

Correspondence to: L. Zhang

Polyploidy, although rare in animals, has been found in most major groups that possess an asexual mode of reproduction (reviewed by Suomalainen et al. 1987; Beaton and Hebert 1988; Walsh and Zhang 1992). The adaptive significance of polyploidy in animals remains unclear. Our current knowledge about the effects of polyploidy on relative fitness is primarily obtained from studies of higher plants in which polyploidy has been viewed as a major evolutionary force (reviewed by Levin 1983). Demographically, autopolyploid plants have lower developmental rates, delayed reproduction, larger sizes at maturity, longer life spans and reduced fecundities when compared with closely related diploids (Lewis 1980, Van Dijk and Van Delden 1990). Exceptions have also been reported. For example, Lumaret et al. (1987) found that habitat differentiation occurred between diploids and polyploids in the plant *Dactylis glomerata*; an in situ comparison of plant performance showed that where plants of each cytotype were more common, they also had higher fecundity. Physiologically, polyploid plants have been shown to have higher tolerance of many environmental stresses than their diploid relatives (Levin 1983).

Relatively few studies have been conducted with animals and contradictory findings have been reported. For example, tetraploid *Daphnia pulex* have lower developmental rates and smaller broods than their sympatric diploids when measured at 25° C (Weider 1987). These diploids and tetraploids use different microhabitats in nature (Hebert and Emery 1990). In contrast to what is generally found in plants, Browne et al. (1984) reported that three polyploid *Artemia parthenogenetica* populations from India (Madras and Kutch) and Turkey have larger brood sizes and earlier reproduction than two diploid populations from Spain and France under optimal temperature and salinity (25° C, 90 ppt). At a stressful low temperature (15° C), Madras triploids retain a larger brood size; however, at 30° C, the brood size of triploids is larger than Spanish diploids, but smaller than French diploids (Browne et al. 1988). These results suggest that comparisons of the relative fitness

of diploids and polyploids are strongly influenced by the environmental conditions used in the study.

As a first step towards understanding the adaptive significance of polyploidy in *Artemia*, we have compared life history patterns of sympatric diploid and polyploid *A. parthenogenetica* in three populations collected from China, Italy and Spain. To examine how diploids and polyploids respond to environmental changes, the Chinese and Italian populations were selected for further analysis at different salinities and temperatures.

Materials and methods

Origin of the populations

Artemia are the predominant animals in inland salt lakes and coastal salterns where high salinity excludes most predators. A saltern is a series of interconnected artificial ponds having a sea water input. When the salinity in one pond increases to a certain level due to evaporation, the sea water is allowed to flow into the next pond with higher salinity. This transfer creates a salinity gradient between the input ponds and the terminal ponds where commercial sea salt is produced when the sea water becomes oversaturated. *Artemia* are usually found in ponds having salinities higher than 50 ppt (parts per thousand).

Artemia are capable of producing either active nauplii (ovoviviparous broods) or durable cysts (stress-resistant oviparous broods), depending upon genotypic features and environmental conditions (Gajardo and Beardmore 1989; Tackaert and Sorgeloos 1991). Cyclic parthenogenesis has never been reported in this genus. Individuals may produce a succession of broods throughout their life. We collected *Artemia* cysts from a salt pond in the Dong Fang Hong Saltern of the Shandong Peninsula, China (King et al. 1988). In addition, Dr. Patrick Sorgeloos of the *Artemia* Reference Center in Gent, Belgium, provided us with cysts that were collected from salt ponds on the Adriatic Sea at Margherita di Savoia, Italy and from San Lucar on the Mediterranean Sea in southern Spain. The Spanish population is a mixture of sexual (equivalent to *A. tunisiana*, Bowen and Sterling 1978) and asexual individuals (*A. parthenogenetica*). Sexual and asexual forms were separated following the method of Zhang and King (1992). The ploidy level of a given adult female was determined by examining the chromosome numbers of its nauplii following the method of Zhang and King (1992). Morphological differences may also be used to separate diploid and polyploid *Artemia* (Amat 1980). The Chinese population is composed of diploids and pentaploids; the Italian and the Spanish populations are each composed of diploids and tetraploids (Zhang and King 1992). Previous research, based on both allozyme and mtDNA analysis, has shown that asexual *Artemia* of different ploidy levels have monophyletic origin: asexual polyploids evolved from asexual diploids which themselves branched from ancestral sexual diploid *A. tunisiana* or *A. urmiana* (Abreu-Grobois and Beardmore 1982; Browne and Bowen 1991).

Life history determinations of diploids and polyploids under optimal condition of 25° C and 90 ppt salinity

To determine how polyploidy affects life history traits under optimal temperature and salinity, we examined life history patterns of sympatric diploids and polyploids from the three populations at 25±0.5° C and 90 ppt salinity (sea water at 35 ppt+55 g NaCl/l). Reproductive output of *Artemia* has been found to be optimal in this medium (Browne et al. 1984). Animals were maintained under 24-h cool-white fluorescent lighting at an intensity of 4,000–5,000 lux. A unicellular green alga, *Dunaliella tertiolecta*, was grown on 2×F medium at 25±0.5° C and used as food.

Nauplii hatched from cysts on the same day were mass-cultured at low density and then separated to start clonal lines as soon as females showed signs of ovarian development. The ploidy level of each clone was determined by examining the chromosome

Table 1. Life history characteristics (mean±SE) of diploid and polyploid *A. parthenogenetica* at 25° C, 90 ppt. *: $P<0.01$ by an ANOVA comparing the two cytotypes in each population

Characteristic	China		Italy		Spain	
	2N	5N	2N	4N	2N	4N
Cytotype frequency (%)	90	10	38	62	34	66
No. of animals tested for life history traits	19	20	20	20	20	23
Intrinsic rate of increase	0.202±0.019	0.115*±0.011	0.205±0.009	0.142*±0.012	0.100±0.007	0.007*±0.005
Total offspring per female	1744±166	317*±66	776±104	418*±63	1034±156	643*±91
Offspring per brood	177±6	57*±5	151±12	88*±7	129±10	63*±7
% offspring encysted	5.3±2.8	89.5*±6.9	4.2±3.6	55.3*±11.7	55.4±7.0	0*0
Number of broods	9.8±0.9	4.7*±0.8	4.7±0.5	4.4±0.4	7.3±0.9	9.6*±1
Age at first reproduction (days)	26.6±0.9	33.7*±1	29.5±0.7	33.5*±1.1	35.3±0.9	44.6*±1.1
Life span (days)	102.5±7.1	68.4*±5.3	54.9±2.4	60.9±2.9	89.5±6.0	110.8*±8.9

numbers of its offspring. Approximately 20 females were isolated and maintained for each cytotype in each of the three populations (Table 1). Second generation individuals were used for the experiments to reduce maternal effects. Individuals were maintained in 150 ml jars containing 100 ml 90 ppt brine. The medium of each culture was changed daily. After the experimental animals reached reproductive maturity, their offspring were counted and removed from the jars at daily intervals. Numbers of nauplii and diapause cysts produced by each clone were separately recorded. In our study, a "diapause cyst" is defined as an oviparous offspring having a clear, coffee-colored shell which does not hatch in 90 ppt brine for at least one week. Each individual culture was maintained until the parental animal had died. One-way analysis of variance (ANOVA) was used to analyze life history variation within and between cytotypes in each population.

The relative fitness of diploids and polyploids under each treatment was measured by calculating their intrinsic rates of increase (r) following the procedures of Birch (1948). Only nauplii were used for calculating r because cysts require a diapause and do not immediately contribute to growth of the population. The reproductive contribution to r of individuals that produced only cysts was therefore regarded as zero.

Life history determinations of Chinese diploids and pentaploids at a suboptimal salinity of 35 ppt

To determine whether life history patterns measured at 90 ppt (which is common in *Artemia*'s habitats) are similar to those at the suboptimal low salinity of 35 ppt (which is generally regarded as rare in *Artemia's* habitats), we examined life history patterns of three diploid and three pentaploid multilocus genotypes from China. The multilocus genotypes were identified using cellulose acetate gel electrophoresis and will hereafter be referred to as "clones." Three replicates of 5 newly-hatched nauplii were used for each of the six clones. To examine life history patterns after shifting the salinity from 35 ppt to 90 ppt, we transferred newly-hatched nauplii produced in 35 ppt sea water to 90 ppt brine. These nauplii were cultured to maturity and, to eliminate or reduce maternal effects, their first generation offspring were used for the life history determinations. One-way ANOVA was used to compare the life history variation between cytotypes.

Reproductive performance of Italian diploids and tetraploids under various salinities (30 ppt and 180 ppt) and temperatures (25° C and 31° C).

To compare the responses of diploids and polyploids to suboptimal salinities and temperatures, we focused on the survivorship, total fecundity and percentage of cyst production of Italian diploids and polyploids. Nauplii that were hatched from cysts on the same day were mass-cultured at 90 ppt. At an age of 20 days, which is about two-thirds of the prereproductive period (Table 1), diploid and polyploid juveniles (which are morphologically distinguishable) were removed from mass culture and subjected to four treatments (25° C, 30 ppt; 25° C, 180 ppt; 31° C, 30 ppt; 31° C, 180 ppt). About 50 juveniles of each cytotype were used for each treatment. The culture medium was refreshed daily and more than 80% of these juveniles were able to develop to maturity under each treatment. After the animals reached reproductive maturity, ten individuals of each cytotype from each of the four treatments were chosen haphazardly and used to measure fecundity. Numbers of nauplii and cysts produced by each individual were recorded at three-day intervals.

To compare the survivorships of diploids and polyploids under the four treatments, newly-hatched nauplii were used. Since most Italian tetraploids produced cysts in their first three broods at 90 ppt, we had to induce nauplii production by transferring tetraploids to low salinity medium of 30 ppt. About 700 40-day old adults of each cytotype that had been cultured at 90 ppt and 25° C were isolated and transferred to 30 ppt. At this salinity, Italian tetraploids produce most of their offspring as nauplii (Table 5). Five replicates of 100 nauplii from the 30 ppt-adult mixture were used for each treatment. Since most non-senescent mortality occurs in the first nine days of adult life (Vanhaecke et al. 1984), survivorship was measured as the percentage of animals alive at day 20. Responses of the two cytotypes were analyzed using both two-way and three-way ANOVA.

Results

Life history patterns of sympatric diploids and polyploids under optimal temperature and salinity

In this section, we compare the life history patterns of sympatric diploids and polyploids from the three populations under optimal conditions of 25° C and 90 ppt. In all three populations, diploids had significantly higher intrinsic rates of increase, higher net fecundities (total number of offspring per female), larger brood sizes and faster developmental rates than sympatric polyploids (Table 1, $P<0.01$). Cytotypes with longer mean life spans also produced more broods. For example, Chinese diploids had significantly longer life spans and produced more broods than sympatric pentaploids. An opposite pattern was observed in the Spanish population where

Table 2. Life history characteristics (mean ± SE) of the Chinese diploids and pentaploids at 25° C under different salinities (S: ppt). Data are pooled from the three clones of each cytotype. ANOVA significance levels: – : $P>0.01$ *: $P<0.01$

Characteristic	S	Diploids	Pentaploids	ANOVA
Intrinsic rate of increase	35	0.205 ± 0.007	0.225 ± 0.008	
	90	0.190 ± 0.005	0	
Total offspring per female	35	909 ± 97	50 ± 7	
	90	1241 ± 125	197 ± 18	
Offspring per brood	35	157 ± 18	46 ± 18	
	90	161 ± 29	55 ± 6	
% offspring encysted	35	5.8 ± 1.4	38.9 ± 7.4	
	90	5.3 ± 1.4	100	
Age at first reproduction (days)	35	23.0 ± 0.0	17.3 ± 0.5	
	90	29.3 ± 1.3	34.1 ± 1.6	
Life span (days)	35	57.7 ± 9.7	23.7 ± 5.1	
	90	85.0 ± 6.7	66.0 ± 14.1	

tetraploids had longer life spans and more broods than diploids ($P<0.01$, Table 1). Italian diploids and tetraploids had similar life spans and number of broods per female. The frequency of encysted offspring was measured by calculating the ratio of the number of cysts per female to the total number of offspring (including cysts) per female. Chinese and Italian polyploids produced significantly higher percentages of encysted offspring than their sympatric diploids, while an opposite pattern was observed in the Spanish population where tetraploids never produced any cysts ($P<0.01$, Table 1).

To determine if the observed life history patterns at 90 ppt would be altered by a suboptimal salinity of 35 ppt, we looked at life history patterns of three diploid and three pentaploid clones at both salinities. We found that Chinese diploid clones still had significantly higher fecundities, larger brood sizes, longer life spans, and lower frequencies of cyst production at 35 ppt than the pentaploid clones ($P<0.01$, Table 2). At 35 ppt, although both cytotypes had similar intrinsic rates of increase, the pentaploids had significantly faster developmental rates than the diploids (Table 2). Moreover, the three pentaploids clones that produced all of their offspring as cysts at 90 ppt produced most of their offspring as nauplii at low salinity (Table 2).

Responses of Italian diploids and tetraploids to suboptimal salinity and temperature

To evaluate the effects of environmental stress, we focused on the Italian diploids and tetraploids and examined their responses to temperature (25° C and 31° C) and salinity (30 ppt and 180 ppt) variation. All three factors (ploidy level, temperature and salinity) had significant main effects and interactions on our measures of survivorship and reproduction (Table 3).

At a low salinity of 30 ppt, tetraploids had significantly higher survivorship than diploids under both optimal (25° C) and high (31° C) temperatures (one-way ANOVA, $P<0.01$, Fig. 1a). At a high salinity of 180 ppt, diploids had significantly higher survivorship than tetraploids at both 25° C and 31° C ($P<0.01$, one-way ANOVA, Fig. 1a). The interaction of salinity and temperature also had a significant influence on survivorship (Table 4).

Table 3. Results of a three-way ANOVA on the life history traits of Italian diploids and tetraploids. Factors are: ploidy level (P), salinity (S) and temperature (T). Significance levels: –: $P>0.05$, *: $P<0.05$, **: $P<0.01$

Factor	Survivorship	Fecundity	% cyst
P		*	**
S		–	**
T		**	**
P×S		–	**
P×T		**	**
S×T		**	–
P×S×T		**	–

At 30 ppt, although tetraploids had significantly lower fecundity than diploids at 25° C, they had significantly higher fecundity than diploids at 31° C ($P<0.01$ in both cases by one-way ANOVA, Fig. 1b). At 180 ppt, diploids had higher fecundities than tetraploids at both 25° C and 31° C ($P<0.01$, one-way ANOVA, Fig. 1b). The interactive effects of salinity and temperature on fecundity were significant for tetraploids, but not for diploids (Table 4). Salinity level had significant effects on the fecundity of tetraploids, but not on diploids (Table 4). For example, at 31° C, with a change in salinity

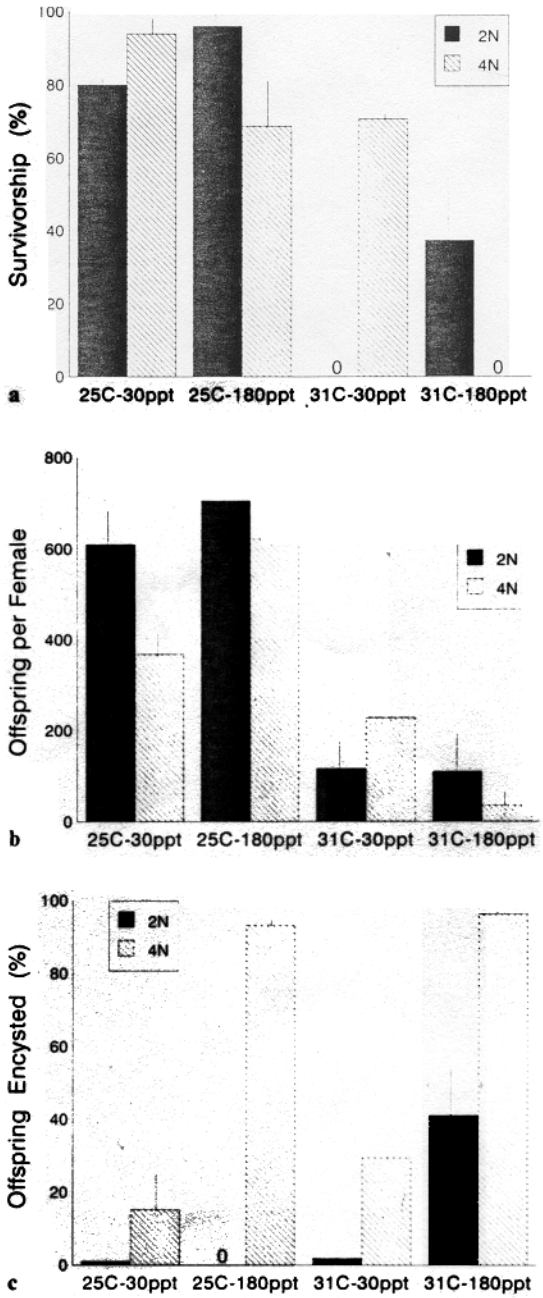

Fig. 1a–c. Effects of different temperature (25° C, 31° C) and salinity (30 ppt, 180 ppt) combinations on the life history traits of Italian diploids and tetraploids. **a** Survivorship; **b** Net fecundity; **c** Percentage of offspring encysted

Table 4. Results of a two-way ANOVA on the life history traits of Italian diploids and tetraploids. Factors are: salinity (S) and temperature (T). Significance levels: −: $P>0.05$, *: $P<0.05$, **: $P<0.01$

Factor	Survivorship		Fecundity		% cyst	
	2N	4N	2N	4N	2N	4N
Temperature		**			**	
Salinity		**			−	
Temperature × salinity		**			−	

from 30 ppt to 180 ppt the fecundity of tetraploids was reduced by 84.4% while that of diploids was only reduced by 5.6% (Fig. 1b).

Tetraploids had higher frequencies of cyst production than diploids at both temperatures and salinities tested ($P<0.01$, one-way ANOVA, Fig. 1c). They produced most of their offspring as cysts at high salinity, and most as nauplii at low salinity. Diploids had low frequencies of cyst production under a wide range of salinities (Table 5). Only at high salinity and high temperature did the frequency of cyst production increase (Fig. 1c). The frequency of cyst production in tetraploids was significantly affected by salinity changes, but not by temperature changes. Diploids showed an opposite pattern (Table 4).

Effects of salinity level on the frequency of cyst production of diploids and polyploids in the three populations

Since *Artemia* cysts are very stress-resistant, frequency of cyst production may be an important component of relative fitness. Table 5 presents a summary of the frequencies of cyst production in the three populations at three salinities (30 ppt, 90 ppt and 180 ppt). Chinese and Italian populations had very similar responses to salinity changes. For polyploids, the percentage of cyst production increased with salinity while diploids in the two populations produced most of their offspring as nauplii irrespective of salinity. Spanish diploids and tetraploids showed an opposite pattern; diploids produced most of their offspring as cysts at intermediate and high salinities while tetraploids produced all of their offspring as nauplii at all salinities tested.

Table 5. Approximate frequency (%) of cyst production of diploids and polyploids in the three populations at optimal temperature (25° C) and different salinities

Salinity (ppt)	China		Italy		Spain	
	2N	5N	2N	4N	2N	4N
30	5.8	38.9[a]	1.1	15.2	7.3	0[b]
90	5.3	89.5	4.2	55.3	55.4	0
180	0	100[b]	0	93.3	100	0[b]

[a] measured at 35 ppt (Table 2)
[b] measured from single mass culture of about 120 individuals

Discussion

Effects of polyploidy on life history patterns

It is well-known that polyploidization within an asexual lineage is associated with an increase in heterozygosity (reviewed by Suomalainen et al. 1987). This is also the case in *Artemia*: polyploids have higher levels of heterozygosity than diploids (Abreu-Grobois and Beardmore 1982, Zhang and King 1992). In addition, genetic divergence has also occurred following the polyploidisation in *Artemia*; at some loci sympatric diploids and polyploids in our study have different alleles (Zhang and King 1992). Life history differences between diploids and polyploids may therefore have their origin in allelic divergence and increased heterozygosity as well as in the increased DNA content.

It has been suggested that there is a strong inverse correlation between DNA content and developmental rate in eucaryotes (reviewed by Levin 1983; Cavalier-Smith 1985). In animals, most of the evidence for this inverse correlation is from observations made under laboratory conditions that usually favor diploids (Goin et al. 1968; Weider 1987). Our results from 25° C, 90 ppt salinity (which are common levels in *Artemia*'s habitats) support this generalization. However, when cultured in 35 ppt sea water (which is rare in *Artemia*'s habitats) at 25° C, the three pentaploid clones from China have faster developmental rates than their three sympatric diploid clones. Browne et al. (1984) also reported higher developmental rates for Indian polyploid *Artemia* than Spanish and French diploid *Artemia* at 25° C and 90 ppt salinity. Thus while ploidy level may have a strong effect on developmental rates, the expression of this effect is greatly influenced by environmental conditions.

A second generalization, based on studies of many plant species and a smaller number of animals (Dewey 1980; Schultz 1980; Weider 1987), is that polyploids have larger body size at maturity and reduced fecundities. Our measures at 25° C, 90 ppt support these studies; diploids had smaller brood sizes and higher fecundity than their sympatric polyploids. Polyploids have larger cyst sizes and body size at maturity than diploids (Zhang and King, unpub. data; Amat 1980; Wang et al. 1990). However, a low salinity of 30 ppt and high temperature of 31° C, Italian tetraploids have significantly higher fecundity than sympatric diploids. Thus the relationship between fecundity rates and cytotype may differ with both population and environment.

Similar conclusions may be drawn from the relationship we observed between life span and cytotype. For example, Chinese and Italian polyploids had shorter life spans while Spanish tetraploids had a longer life span than their sympatric diploids. In agreement with the work on allopatric diploid and polyploid populations

(Browne et al. 1988), our results further demonstrate that the comparisons of life history traits between diploids and polyploids can be altered by the environmental conditions tested.

Nevertheless, our results show that at salinities that are common in *Artemia*'s habitats, polyploids have lower developmental rates, smaller brood sizes and lower fecundities than sympatric diploids. Moreover, under the same conditions diploids consistently have higher intrinsic rates of increase than sympatric polyploids. Therefore it seems reasonable to suggest that under optimal conditions diploids generally have higher fitness. It is primarily in suboptimal or marginal environments that polyploids sometimes appear to have an advantage.

Responses of diploids and polyploids to environmental stress

A. Cyst production. Under some circumstances cyst production in *Artemia* is an important component of fitness because encysted embryos are protected from many environmental stresses. Cysts may act as a "seed pool" permitting population survival in periodically stressful or unpredictable environments (Versichele and Sorgeloos 1980; Lenz and Browne 1991). However, when intraspecific competition is important, high frequencies of cyst production may be disadvantageous because *Artemia* cysts require a diapause (from several days to several months) and do not immediately contribute to the growth and competitive ability of the parental clone. Different genotypes or populations may have different rates of cyst production (Browne et al. 1984; Gajardo and Beardmore 1989) and it has been reported that cyst production is usually induced by adverse conditions such as stressful salinities or low oxygen concentrations (Tackaert and Sorgeloos 1991). In our study, both cytotype and population had significant effects on the frequencies of cyst production. Under salinities common in coastal salterns (>60 ppt), Chinese and Italian polyploids produced most offspring as cysts while their sympatric diploids produced most of their offspring as nauplii (Table 5). This relationship is reversed in Spanish tetraploids and diploids. Furthermore, cytotypes that have high frequencies of cyst production at intermediate and high salinities may shift to produce nauplii at low salinities (Table 5).

The different patterns of cyst production by Spanish and Italian tetraploids are particularly interesting. Measures of the genetic similarity of the two groups show that they are closely related (Nei's standard genetic identity I=0.964, Zhang and King 1992) even though their collection sites are rather widely separated (41° 25'N – 16° 05'E for the former, vs. 36° 43'N – 6° 23'W for the latter). As indicated in Table 1, tetraploids from the two populations differ in most of the life history traits examined. Moreover, Italian tetraploids produced most of their offspring as cysts while Spanish tetraploids produced all of their offspring as active nauplii (Table 5). Thus the life history characteristics of this cytotype appear to have undergone extensive geographical divergence.

B. Polyploidy as a buffer against environmental stress. A number of investigators have proposed that polyploids are genetically better buffered against environmental stress than closely related diploids (see, for example, Levin 1983; Suomalainen et al. 1987). This perception is based largely on the observation that polyploids tend to be found in extreme environments such as high latitudes, high elevations, or arid areas when compared with diploid relatives (Bierzychudek 1985; Suomalainen et al. 1987; Beaton and Hebert 1988; Zhang and Lefcort 1991). However, the physiological responses of diploids and polyploids to stressful conditions do not show a consistent pattern of polyploid superiority as might be expected from the geographical distributions. For example, diploid and triploid salamanders (*Ambystoma laterale-texanum*) have similar thermal tolerance limits, while triploid fish (*Poeciliopsis monacha-lucida*) have lower resistance to heat stress but higher resistance to cold stress than diploids (Schultz 1982; Licht and Bogart 1989). Tetraploid *Daphnia pulex* from the low arctic of Canada have lower tolerance of high temperatures than the temperate diploid populations (Macisaac et al. 1985). Moreover, at a stressful high temperature of 30° C, Madras (India) triploid *Artemia* do not have substantially higher fitness than Spanish and French diploids (Browne et al. 1988).

Our data support the conclusion that there is a positive relationship between polyploidy and resistance to environmental stress. As mentioned earlier, Chinese pentaploids had higher developmental rates and similar intrinsic rates of increase than diploids at low salinity and optimal temperatures. The polyploid *Artemia* in our study had higher survival rates than sympatric diploids after a short exposure to cold and heat shocks irrespective of the culture salinities (Zhang and Lefcort 1991, Zhang and King per. obs.). Polyploids can survive a 30-minute heat shock of 41° C, develop to maturity and reproduce while diploids can not (Zhang and King, unpub. data). Obviously, this difference may give polyploids at least short-term advantages over sympatric diploids, because most coastal salt ponds are shallower than one meter and their temperature approaches lethal levels on hot summer afternoons. However, this short-term advantage may not apply to sublethal temperatures unless the thermal stress is also combined with low salinity stress. At low salinities and high temperatures, Italian tetraploids had both higher survivorship and higher fecundity than diploids (Fig. 1a and b).

These results indicate that polyploids have advantages over their sympatric diploids in utilizing spatially or temporally marginal environments. Additional field work is necessary to determine the microgeographic distributions of the two cytotypes within their salterns as well as the adaptive significance and ecological relevance of our observations.

Our data clearly support a positive relationship between polyploidy and resistance to environmental stress. Note, however, that identifying stressful environments in physiological terms is a tautological process and different measures of stress response may lead to different categorizations. Furthermore, if our results are typical

it may be the interaction between different environmental elements, rather than their separate effects, that produces physiological stress and decrease in fitness.

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